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Fundamental principles of the effect of habitat fragmentation on species with different movement rates

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Article impact statement: Fragmentation and high rates of locomotion have a negative impact on population abundance, even where habitat loss is low.

Abstract

Habitat loss and fragmentation have independent impacts on biodiversity; thus, field studies are needed to distinguish their impacts. Moreover, species with different locomotion rates respond differently to fragmentation, complicating direct comparisons of the effects of habitat loss and fragmentation across differing taxa and landscapes. To overcome these challenges, we combined mechanistic mathematical modeling and laboratory experiments to compare how species with different locomotion rates were affected by low (∼80% intact) and high (∼30% intact) levels of habitat loss. In our laboratory experiment, we used *Caenorhabditis elegans* strains with different locomotion rates and subjected them to the different levels of habitat loss and fragmentation by placing *Escherichia coli* (*C. elegans* food) over different proportions of the Petri dish. We developed a partial differential equation model that incorporated spatial and biological phenomena to predict the impacts of habitat arrangement on populations. Only species with low rates of locomotion declined significantly in abundance as fragmentation increased in areas with low ($p = 0.0270$) and high ($p = 0.0243$) levels of habitat loss. Despite that species with high locomotion rates changed little in abundance regardless of the spatial arrangement of resources, they had the lowest abundance and growth rates in all environments because the negative effect of fragmentation created a mismatch between the population distribution and the resource distribution. Our findings shed new light on incorporating the role of locomotion in determining the effects of habitat fragmentation.

KEYWORDS
fragmentation, habitat loss, locomotion rate, partial differential equations, theory, experiment

INTRODUCTION

Amid the ongoing increase in species extinctions, habitat loss and fragmentation are major threats to biodiversity (Luo et al., 2022). Fragmentation is correlated with landscape- and patch-level changes, including decreased total habitat area and quality and increased isolation of habitat patches and ratio of habitat edge to habitat area. These changes can negatively affect species diversity (Fahrig, 2002, 2017, 2019; Keyghobadi, 2007). Habitat fragmentation is difficult to define precisely due to its multitude of effects. Typically, habitat fragmentation is viewed from 2 perspectives: first, fragmentation as a process involving the loss and breaking apart of habitat as a result of habitat degradation or destruction (Fahrig, 2017; McGarigal & Cushman, 2002), and, second, fragmentation as a process separate from other forms of habitat loss (throughout denoted as fragmentation per se) (Fahrig, 2003, 2017). In this context, for a given fixed amount of habitat, a more fragmented landscape will have smaller, more numerous habitat patches and a greater total length of habitat edge (Fahrig, 2003, 2017). The lack of consistency in defining and quantifying fragmentation and the uncertainty about whether observed effects are caused by fragmentation or habitat loss, or both, have resulted in ongoing debates concerning the relative impacts of fragmentation (Fahrig, 2017; Fletcher Jr. et al., 2018).

The impacts of fragmentation on biodiversity, given that the observed impacts of habitat fragmentation are varied, have been debated. Some species may be negatively affected by

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fragmentation (Fletcher Jr. et al., 2018), whereas others may benefit (Fahrig, 2017; Rybicki et al., 2020). The counterintuitive positive effects of fragmentation have been attributed to, for example, increases in functional connectivity, diversity of habitat types, persistence of predator–prey systems, and decreases in intra- and interspecific competition (Rybicki et al., 2020). Variation in observed impacts is likely due to the challenges of conducting manipulative field studies at spatial scales relevant to conservation that distinguish and identify the impacts of fragmentation and habitat loss (Laurance et al., 2002). Considering that it is laborious and costly to manipulate large landscapes to overcome these problems (Debinski & Holt, 2000), alternative methodologies are required to determine the effect of loss and fragmentation of a fixed amount of habitat on population dynamics.

We aligned this work with the second perspective, fragmentation per se (Fahrig, 2003, 2017). We examined the effects of varying the arrangement of usable habitat given the same fixed area of total usable habitat. We examined fragmentation based on the quality of the patches in the environment. As nonhabitat gets closer to the center of the landscape, we considered that the environment becomes more fragmented. Further, it is critical to consider that species respond differently to the same level of fragmentation according to their traits. For instance, habitat specialists, species with large body sizes, species at higher trophic levels, and species that do not rely heavily on mutualist species are expected to go extinct first when habitat occurrence decreases (Didham, 2010). However, understudied traits important for understanding and estimating fragmentation effects in the field are dispersal and locomotion strategies, which are fundamental features of life (Nathan, 2008; Zhang et al., 2022). We used locomotion and dispersion as generic synonyms to describe an organism's ability to move from one location to another and considered that a relatively higher rate of locomotion corresponds to a relatively greater area traveled in a landscape. Locomotion is increasingly considered a critical process in ecological dynamics and is used to predict species' adaptation and responses to changing environments (Clobert et al., 2012) given that different movement speeds determine how easily an organism can travel between patches and affect the likelihood of finding patches with better resource or leaving resource-rich patches to avoid, for example, competition or predation (Dickie et al., 2023; Squires et al., 2013; Zhang et al., 2023). Fragmentation and human activities also alter organismal movement patterns. For instance, human actions have widespread impacts on animal movements (Doherty et al., 2021). Additionally, fragmentation reduces species' movement rates (Diffendorfer et al., 1995), and provision of habitat corridors can increase the ability of organisms to move (Li et al., 2021, 2023). Given the importance of ongoing changes in organismal movement strategies under human activities, understanding how different movement strategies determine species' success and survival under fragmentation is essential (Rohwäder & Jeltsch, 2022).

Mathematical models have been used to study habitat fragmentation relative to habitat loss. Modelers have described the effects of removing a proportion of total available habitat with ordinary differential equations (ODEs) (Tilman et al., 1994). However, this framework assumes a spatially homogeneous environment (only the total amount of habitat removed is considered, making an implicit equivalence between any possible arrangement of habitat) and is therefore not applicable to questions of fragmentation. Discrete patch models (i.e., implicit spatial models [DeAngelis & Yurek, 2017]) allow researchers to investigate the impact of habitat loss in relation to habitat connectivity (Dytham & Travis, 2012). To quantify habitat fragmentation per se, some have used statistical tests and simulated environments (Hargis et al., 1998; Wang et al., 2014). In both cases, an explicit spatial structure or an explicit biological mechanism is lacking (e.g., statistical analysis and correlations alone are insufficient for generalization). It is essential to include both given the close relationship among physical space, varying habitat arrangements, and species characteristics (Fahrig, 2019; Fletcher Jr. et al., 2018). To incorporate explicit spatial and biological phenomena, we used the theory of partial differential equations (PDEs) to describe the dynamics of a dispersing population, where dispersal is described via linear diffusion arising from an assumption of Brownian motion. The PDE description of a dispersing population can be derived from biologically motivated first principles (Cantrell & Cosner, 2004). Particularly, the notion of eigenvalues of linear operators describes the way dispersing populations with a prescribed movement pattern use spatiotemporally distributed resources and holds significant potential for use in describing and predicting the impacts of habitat arrangement (e.g., fragmentation) on such populations.

Ecological and mathematical theories predict that fragmented areas select for either slow or fast moving species (Cote et al., 2017; Fahrig, 2007), but there have been no rigorous empirical studies to determine responses of different movement rates to fragmentation. For instance, some suggest that species with large movement ranges, enabling them to colonize patches beyond the distance of correlated environmental fluctuations, should have a relatively lower extinction risk in highly fragmented habitats (Fahrig, 2017; Van Houtan et al., 2010). Others suggest that fragmentation effects should be weak for species with low or high dispersal rates and strong for species with intermediate dispersal rates, where dispersal is defined by the probability of moving farther over time steps (Fahrig, 1998). We found only one empirical study related to these hypotheses. It showed that 5 years after fragmentation, isolated species are more likely to decline than species that are not isolated (Davies et al., 2000), indicating that species with faster dispersal may respond better to fragmentation. Hence, it is crucial to create new and rigorous empirical methods to isolate the effects of habitat degradation or destruction and habitat fragmentation and to determine the role of locomotion in species survival under different fragmentation regimes. Such empirical work can be used to validate mathematical theories. These tested theories can be used to develop a robust theory of organisms' general responses to habitat change and fragmentation, especially where experimental work is difficult.

We analyzed a linear, mechanistic PDE model under an assumption of random (Brownian) movement and variable spatial arrangements of food. We then made several theoretical predictions related to the intrinsic population growth rate, depending on the combination of locomotion rates and resource arrangements. Then, we tested theoretical predictions in laboratory experiments with *Caenorhabditis elegans*. In these experiments, we manipulated patterns of habitat loss and fragmentation and locomotion rates of *C. elegans* to identify the joint impacts of habitat change and locomotion rates on population abundance. Under an assumption of random movement locomotion of *C. elegans*, we tested mathematically and experimentally 3 key hypotheses suggested by results in existing empirical and theoretical literature.

Hypothesis 1. Habitat amount alone is insufficient to predict population growth rates; therefore, fragmentation per se affects population growth rates.

Hypothesis 2. Increased fragmentation and higher rates of dispersal, when controlling for habitat amount, have a negative impact on population growth rates.

Hypothesis 3. Fragmentation per se has a strong negative impact, even under low levels of habitat loss.

Overall, we sought to shed light on habitat fragmentation impacts and potential mitigation, pressing concerns in biodiversity conservation.

METHODS

Model framework

We considered a population adopting diffusive movement with constant rate $d > 0$ moving in a one-dimensional environment, where the intrinsic (possibly spatially dependent) growth rate is denoted by $r(x)$, where x represents the location. This modeling framework is most aptly applied to species whose mechanism of locomotion can be adequately described by, at least as a first approximation, linear diffusion. Diffusion equations are widely applicable, deterministic approximations of particles or agents moving randomly at the individual level but predictably at the population level (Cantrell & Cosner, 2004; Okubo & Levin, 2013). This modeling framework allows one to explore interactions between heterogeneous population growth and decay and diffusive movement strategies. Our modeling framework is readily generalizable to different movement strategies aside from or in addition to linear diffusion.

We assumed that the intrinsic growth rate of *C. elegans* correlates closely with the nutrient, food, and resource distribution (Zhang et al., 2022). We considered an experimental setup in which a cross section of the 2-dimensional Petri dish represents a one-dimensional PDE (Figure 1, where horizontal cross sections are identical). We denoted the spatial average of the function $r(x)$ over $(0, L)$ divided by $\bar{r}$ as

$$\bar{r} = \frac{1}{L} \int_0^L r(x)\, dx, \tag{1}$$

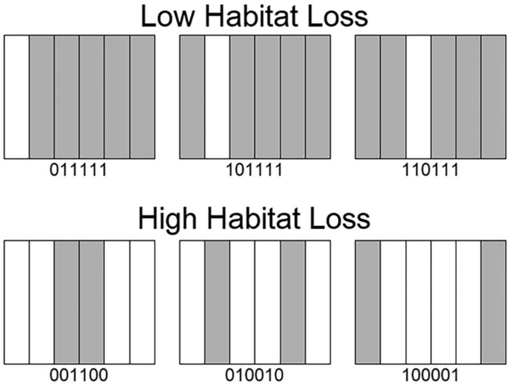

FIGURE 1 Six habitat fragmentation environments (gray columns, habitat with food [1]; white columns, habitat without food [0]). Fragmentation increases from left to the right.

where L is the side length of the Petri dish.

For example, we defined a fragmented environment with steep edges between habitat and matrix by

$$r(x) = \begin{cases} r_0, & \text{for } x \text{ belonging to habitat regions,} \\ -1, & \text{for } x \text{ belonging to matrix,} \end{cases} \tag{2}$$

where $r_0 > 0$ is constant and regions of habitat versus matrix are relatively connected (Appendix S1). This yields

$$\bar{r} = \frac{r_0 A - B}{L}, \tag{3}$$

where A is the total area of the remaining habitat and B is the total area of the matrix. For simplicity, we considered the suggestive situation of $r_0 > 0 > \bar{r}$ (i.e., the environment consists of habitat [$r = r_0$] and matrix [$r = -1$]) and that the ecosystem is not viable on average ($\bar{r} < 0$). This simple formulation features a principal eigenvalue (Cantrell & Cosner, 1989, 2004) that is used to estimate the effective growth rate of the population for small population levels (Britton & Britton, 2003; Cantrell & Cosner, 2004). This quantity allowed us to determine some fundamental rules in a general setting. It is very difficult to determine theoretical properties of this growth rate with respect to arbitrary arrangements, but some results exist in the mathematical literature (Kao, Lou, & Yanagida, 2008; Lou & Yanagida, 2006) that provide insight into which arrangements maximize the growth rate for a fixed amount of habitat.

We estimated population abundance at time t as

$$N(t) = N_0 \exp\left(r_{\text{eff}} t\right), \tag{4}$$

where N_0 is the initial population abundance and r_{eff} is the effective population growth rate (in the mathematical literature, this is commonly denoted by μ_1, as in our Appendices). This calculation is based on the assumption that there are no density-dependent effects in the experiment. For the experimental timescale considered, we assumed that such density dependence does not greatly contribute to the effective growth rate. In fact, r_{eff} is obtained via the linearization of a nonlinear growth functional response and is therefore most appropriately described as an effective growth rate for small population sizes, as is the case at the beginning of the experiment. Under this assumption, the r_{eff} of such a diffusing population is a real number that depends on its locomotion rate (d) and on the spatially dependent intrinsic growth rate $r(x)$. It is characterized as the dominant eigenvalue of a particular elliptic eigenvalue problem (Cantrell & Cosner, 2004; Okubo & Levin, 2013; Skellam, 1951), and it can be shown that

$$\bar{r} < r_{\mathrm{eff}} < \max r\left(x\right).$$

Technical details are in Appendix S1. The r_{eff} is a single quantity used to assess impacts of locomotion rates in various environments. If $r_{\mathrm{eff}} < 0$, the population is predicted to decline; if $r_{\mathrm{eff}} > 0$, the population is predicted to grow. Moreover, large rates of diffusion lead to the minimum growth rate, which is the average value $\bar{r}$. Small rates of diffusion can counteract the effect of fragmentation to achieve maximum growth, that is, r_{eff} approaches the maximum value of $r(x)$ as d approaches 0 (e.g., Lam & Lou, 2022). Because r_{eff} combines the effect of dispersal rate and resource arrangement, it allowed us to define a measure of the length scale of fragmentation (see Equation 5). Roughly speaking, we sought the largest possible dispersal rate such that the r_{eff} would be greater than the midpoint between the minimal and maximal r_{eff} predicted by r_{eff}. This fragmentation length scale provides a direct connection between the average size of the fragmented habitat patches and the dispersal rate of the population considered. Although we applied this measure to a single nematode population that we assumed to have purely diffusive movement, this modeling framework (including the fragmentation length scale defined in Equation 5) is readily generalizable to any scenario featuring a dispersing population with a combination of diffusive and biased movement strategies (Belgacem & Cosner, 1995). In the general case, the movement strategies will be associated with a general elliptic linear operator that features a dominant eigenvalue (Lam & Lou, 2022). We sought a minimalistic model that would appropriately capture the diffusive movement of nematodes. We did not address the questions of more complex movement strategies for nematodes (or other organisms) and their relation to fragmented environments.

Caenorhabditis *elegans* strains

We developed a series of laboratory experiments with *C. elegans* to help further develop and validate our model. *Caenorhabditis elegans* is a species of nematode that has been widely used as a model organism in biology and ecology. *Caenorhabditis elegans* is fed on OP50 *Escherichia coli*, which provides an opportunity to simulate and manipulate habitat loss and fragmentation by altering the coverage area and arrangement of *E. coli* on a Petri dish. *Caenorhabditis elegans* is also useful for studying animal locomotion strategies (Flavell et al., 2013) due to its ability to be grown easily, quickly, and cheaply and the diversity of mutant strains. Three strains of *C. elegans* with different locomotion rates were used in the experiment: MIA470 tax-2(p694) I (vsIs183 lite-1[ce314] lin-15[n765ts] X); MIA471 tax-2(p694) I (egl-4(n478) IV); and MIA472 tax-2(p694) I (pdfr-1[ok3425] III). Specifically, the locomotion rates rank as MIA 472 (low) < MIA 470 (intermediate) < MIA 471 (high) (Zhang et al., 2022). Compared with the slow-moving strain, which tends to stay in a small area, the fast-moving strain moves much faster across a bacterial lawn and turns infrequently (Flavell et al., 2013). The 3 strains have only random movement and do not have directed movement toward resources, which is consistent with the assumptions made in the mathematical model formulation. There were no intrinsic fitness (brood size) differences among strains, except locomotion rates (Zhang et al., 2022).

Culture maintenance

We grew *E. coli* by incubating the strain in B broth for at least 24 h at 35°C. During incubation, *E. coli* medium was kept in a 4°C refrigerator for up to 1 month. We maintained and cultured *C. elegans* in polystyrene Petri dishes (60 × 15 mm). We placed 3–5 L_4 life stage worms on each plate containing 100 μL of *E. coli*. Plates incubated at 20°C for approximately 96 h to allow time for worms to reproduce and reach maturity. To continue the process, we transferred 3–5 L_4 life stage worms to new plates with fresh *E. coli* to prevent overpopulation.

Fragmentation patterns

Fragmentation experiments were performed in square Petri dishes (100 × 100 mm) that were subdivided into 6 consecutive columns. These columns defined the areas where *E. coli* were placed uniformly or were not placed. Using different sizes of 3D-printed blocks, we created different arrangements of *E. coli* for different dishes to represent different arrangements of habitat for the nematodes (Figure 1).

Experimental trials

In Trial 1, we covered 5 out of 6 columns with *E. coli* to represent low levels of habitat loss. We created 3 intensities of fragmentation by moving the empty patch closer to the center of the plate to increase fragmentation intensity. For low-intensity fragmentation, all columns were covered with *E. coli* except the first one (011111) (0, no food; 1, with food). For intermediate intensity fragmentation, all columns except the second one were covered with *E. coli* (101111). For high-intensity fragmentation, all columns except the third one were covered with *E. coli* (110111) (Figure 1).

In Trial 2, we covered 2 out of 6 columns with *E. coli* to represent the condition of high levels of habitat loss. We created 3 intensities of fragmentation by changing the distance between the 2 columns with *E. coli*. For low-intensity fragmentation, we covered columns 3 and 4 with *E. coli* (001100). For intermediate intensity, we covered columns 2 and 5 (010010) with *E. coli*. For high intensity, we covered columns 1 and 6 (100001) with *E. coli* (Figure 1). There were 5 replicates of each of the 3 strains in each environment.

Data collection

In each experimental treatment, *E. coli* was placed on plates and allowed to dry for 1–2 days. We then added 3 L_4 nematodes to the center of each Petri dish to ensure the worms had an equal chance of moving to any direction on the Petri dish and to eliminate potential effects of initial conditions. After placing on plates, worms were grown in a 20°C incubator for 120 h, at which time they had depleted most *E. coli* on each plate, but there was still sufficient food to avoid competition. At this point, the majority of the worms had reached the L_4 stage. This stage and adult animals are easiest to score under the microscope. Upon completion of incubation, worms were placed in a 4°C refrigerator to prevent further growth and stop movement to ease data collection accuracy. Population abundance was measured by counting the total number of individual worms in the L_3 to adult stages on each plate.

Statistical analyses

There was no random effect given our experiment design (2 treatments [fragmentation and locomotion] under each level of habitat loss). For each combination of fragmentation and locomotion, there were multiple replicates, not repeated measures over time. Hence, the main and interactive effects of fragmentation and locomotion on population abundance were analyzed by generalized least squares (GLS) models under the 2 levels of habitat loss. Instead of the Akaike information criterion, we focused on the assumptions of linear regression analyses. The assumption of equal variance was not satisfied because the residual plots showed heterogeneous variances of model residuals among the levels of fragmentation. Thus, in the GLS models, we added a component that allowed for heterogeneous residual variances between the fragmentation levels with the varIdent function from nlme package. Outliers were identified based on Cook's distance, and there were 5 outliers in the case of high levels of habitat loss (the 3 fast moving strains in the high fragmentation, the slow strain in the medium fragmentation, and the medium strain where levels of fragmentation were low). These outliers were removed from further analyses, which had minimal effects on results because there were no changes in the directions (or patterns) of locomotion and fragmentation effects. The above analyses were conducted in the nlme package in R 3.1 (Pinheiro et al., 2012). Moreover, we made multiple comparisons of the population abundance among the different combinations of fragmentation and locomotion levels. The multiple comparisons were based on the overall false discovery rate method to control the proportion of falsely significant differences in the multiple comparisons (Verhoeven et al., 2005). We conducted this analysis in emmeans in R 3.1 (Lenth et al., 2018).

At each level of habitat loss, we determined the correlations between population abundance and distance to food and compared the correlation slopes among the 3 locomotion levels. The above analyses were conducted with GLS models, population abundance was used as the response variable, and distance to food and locomotion were used as predictor variables. We defined the distance of the column with food as 1, the distance of the column next to the column with food as 2, and the distance of the column 2 columns away from the column with food as 3. The greater the number, the farther the column was from food. We used the same steps and R packages described above to build the models and check the assumptions. A significant interactive effect of the 2 predictor variables would suggest significant variation in the correlation slopes between the 3 locomotion levels.

RESULTS

Theoretical

We let $r(x)$ be a function describing a cross section of the distribution of resources on the Petri dish and $r_{\mathrm{eff}}[d, r(x)]$ be the effective growth rate characterized as the previously mentioned principal eigenvalue (see footnote in Appendix S1). Corresponding to the experimental design, we choose $r(x)$ such that it was 0 in regions without food and 1 in regions with food. The r_{eff} depended on the dispersal rate (d) and resource arrangement $r(x)$. Recall that the effective growth rate was bounded from below by average value ($\bar{r}$) and reached the maximum value ($\max r[x]$) when d tended to zero. In general, for more fragmented landscapes, a smaller diffusion rate was needed to maintain a high effective growth rate (r_{eff}). The mechanism behind the negative influence of dispersal in a fragmented environment can be understood through existing concepts of the critical patch size in a patch with a hostile boundary (Cantrell & Cosner, 2004; Kierstead & Slobodkin, 1953). In such cases, a higher rate of dispersal effectively increases how often the population runs into the hostile boundary. In our case, a higher rate of dispersal increased the amount of time the population spent in the less favorable regions. These considerations led to the following definition of fragmentation length scale:

$$d_{\mathrm{frag}}\left[r\left(x\right)\right] := \sup\left\{ d > 0 \left| r_{\mathrm{eff}}\left[d, r\left(x\right)\right] \geq \frac{\max r\left(x\right) + \bar{r}}{2} \right. \right\}, \tag{5}$$

where $d_{\mathrm{frag}}[r(x)]$ gives the precise rate of dispersal at which the effective population growth rate is exactly at the midpoint between the smallest and largest r_{eff} possible for the given $r(x)$. For dispersal rates smaller than $d_{\mathrm{frag}}[r(x)]$, the r_{eff} was larger than this middle value, whereas for dispersal rates larger than $d_{\mathrm{frag}}[r(x)]$, the r_{eff} was smaller than this middle value.

For a heterogeneous environment, $d_{\mathrm{frag}}[r(x)]$ was always between 0 and $+\infty$. However, when the environment was homogeneous, $r_0 = \max r(x) = \bar{r} = r_{\mathrm{eff}}[d, r(x)]$ for all $d > 0$, and so $d_{\mathrm{frag}}[r(x)] = \infty$. This suggested that r_{eff} was identical for any rate of locomotion: there was no theoretical benefit to a slower rate of dispersal in a homogeneous environment. Then, based on Cantrell and Cosner's (1989) results, we deduced the precise criteria for $d_{\mathrm{frag}}[r(x)] = 0$ (see theorem 1 in Appendix S1). This condition required that the environment become increasingly fragmented, suggesting an intimate connection between fragmentation of the environment and fragmentation length scale (defined above). This brief exploration of the possible extremes of the fragmentation length scale led to the following conclusion: an environment becomes more fragmented as its fragmentation length scale decreases. It is therefore instructive to define, for each $\alpha > 0$, the following rescaled version of $r(x)$:

$$r_\alpha(x) := r(\alpha x). \tag{6}$$

The parameter α controls the level of fragmentation of the environment while allowing the total amount of habitat to remain constant, such that as α increases, the level of fragmentation also increases. For example, one may observe the scaling relationship between the arrangements 001100 and 010010, where the second arrangement is 2 copies of the first with each copy half the original size.

The larger the value of α, the more fragmented the landscape. We observed the following analytical scaling relationship between the fragmentation of the environment and the diffusion rate of the population:

$$r_{\mathrm{eff}}(d, r_\alpha) = r_{\mathrm{eff}}\left(\alpha^2 d, r\right). \tag{7}$$

This suggested that fragmenting the landscape by a factor of α was equivalent to increasing the dispersal rate by a factor of α^2, in terms of the change in r_{eff}. For example, choosing $\alpha = 2$ was equivalent to increasing the dispersal rate by a factor of 4. Thus, fragmentation had a negative impact on r_{eff} and consequently on population abundance according to $N(t)$. We connected the fragmentation length scale with the reduction principle as follows.

For a given heterogeneous environment $r(x)$, there held

$$d_{\mathrm{frag}}[r_\alpha(x)] = \frac{1}{\alpha^2} d_{\mathrm{frag}}[r(x)] \tag{8}$$

for any $\alpha > 0$. Moreover,

$$\lim_{\alpha\to\infty} d_{\mathrm{frag}}[r_\alpha(x)] = 0 \text{ and } \lim_{\alpha\to 0^+} d_{\mathrm{frag}}[r_\alpha(x)] = \infty. \tag{9}$$

This meant that as the environment became increasingly fragmented ($\alpha \to \infty$), the resource patches became narrower, and only populations with a relatively small diffusion rate maintained a reasonable r_{eff} to persist, whereas a fast-diffusing population (relative to d_{frag}) had a minimal growth rate (close to $\bar{r}$) and therefore could not persist whenever $\bar{r} < 0$.

These insights directly supported our first 2 hypotheses. Because the average amount of available resources was fixed, the fact that the r_{eff} changed with respect to changes in food arrangement indicated that fragmentation had a significant influence on the population growth rate. Fragmentation (as measured by the parameter α) negatively affected a diffusing population through a decrease in the populations' r_{eff}. Even with low levels of habitat loss, we observed this phenomenon: moving the empty region into the center of the dish decreased the population growth rate. This introduced a caveat for the validity of Hypothesis 3. There were always detectable differences in population growth rates even where levels of habitat loss were low, but the difference was less significant relative to when levels of habitat loss are high. We made this more precise in the following corollary, a direct consequence of the scaling relationship above.

If $r(x)$ is a given function and $r_\alpha(x)$ is as above, then

$$\lim_{\alpha\to\infty} r_{\mathrm{eff}}[d, r_\alpha(x)] = \bar{r} \text{ and } \lim_{\alpha\to 0^+} r_{\mathrm{eff}}[d, r_\alpha(x)] = \max r(x). \tag{10}$$

This suggested that r_{eff} changed when the resource was rearranged. A diffusing population had an r_{eff} greater than or equal to the minimal rate of $\bar{r}$. This led to 2 insights. First, r_{eff} could be enhanced simply by increasing the average total resources (e.g., cases of low levels of habitat loss). Second, the r_{eff} could be enhanced provided the population distribution better matched the location or locations where resource levels were close to a maximum. This placed a constraint on the size of the diffusion rate of the population in relation to the fragmentation length scale corresponding to the distribution $r(x)$ and consequently provided a reasonable description of the level of fragmentation of the landscape.

Computational

Figures 2 and 3 provide further insight into d_{frag} for high and low levels of habitat loss. For the top panels of each, $r_{\mathrm{eff}}[d, r(x)]$ was computed for each arrangement depending on the dispersal rate d. In the bottom 3 panels, d_{frag} for each arrangement (vertical dashed pink lines) is shown and is the point of intersection between $r_{\mathrm{eff}}[d, r(x)]$ and the midpoint between the maximum and baseline growth rates. With Equation (8), we obtained d_{frag} for r_2 and r_4 from r_1. For example, $d_{\mathrm{frag}}(r_1) \sim 0.0102$, so with $\alpha = 2$, $d_{\mathrm{frag}}(r_2) = \frac{1}{4} d_{\mathrm{frag}}(r) \sim 0.0026$. This suggested that to maintain the same r_{eff} in an environment that was fragmented by a factor of 2, the species needed to disperse 4 times slower.

From an analytical perspective, the theoretical growth rate for arrangement 001100 was identical to that of arrangement 100001, so we did not include it in Figure 3. This was because of symmetries in the eigenvalue problem itself. Instead, we demonstrated the next order of scaling (010010010010) (bottom right panel of Figure 3), which was not considered experimentally. Although we did not find a precise analytical scaling relationship for the cases with low levels of loss, we could nevertheless

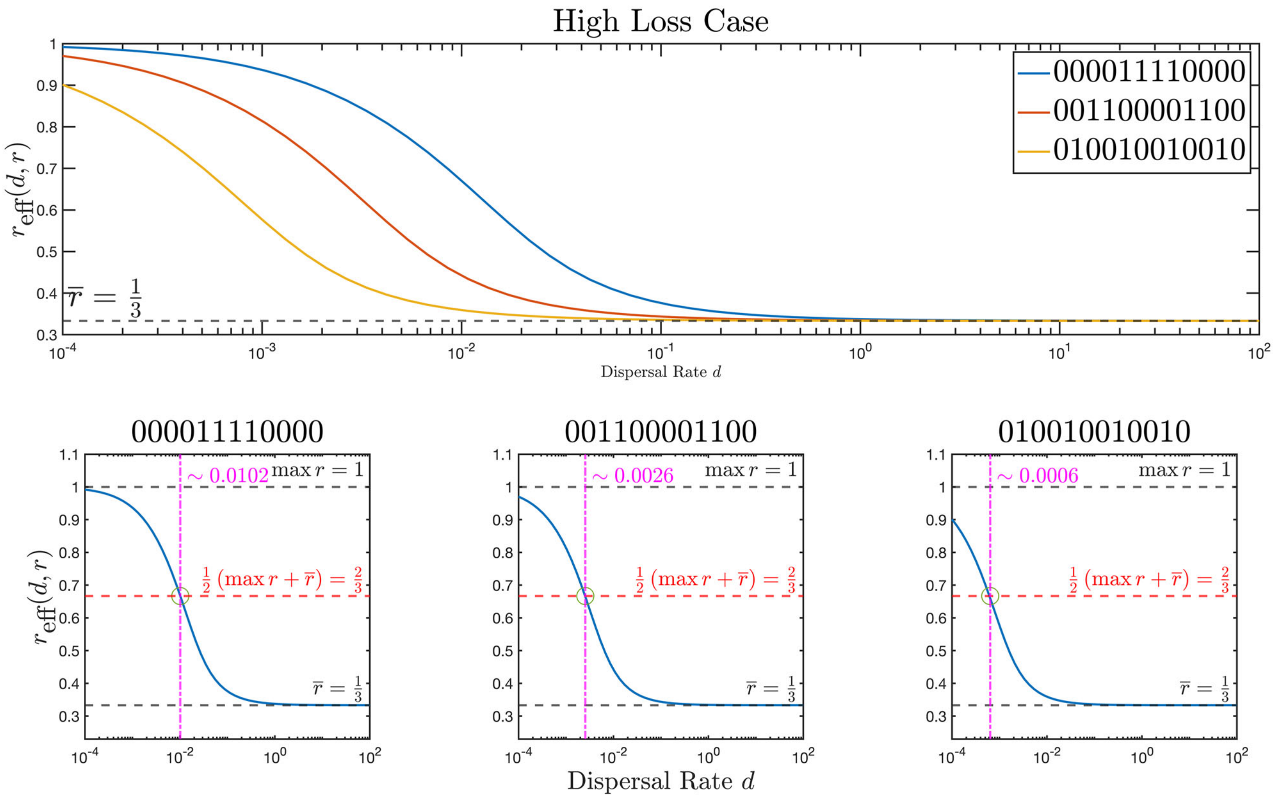

FIGURE 2 Theoretical growth rate of the nematode population ($r_{\text{eff}}[d, r]$) predicted by Equation (4) versus the dispersal rate (d) for 3 cases of high levels of habitat loss and the relationship between different arrangements of nutrient (1, with food; 0, without food) (top panel) and fragmentation length scale (d_{frag}) (vertical dashed pink lines) predicted by Equation (4) for each experimental arrangement displayed in the top panel (bottom panel).

compute the theoretical r_{eff} along with the fragmentation length scale (d_{frag}).

The d_{frag} again decreased as the region without food was moved from the left to the center of the domain. Although the difference between the baseline growth rate and the maximum growth rate was smaller under low levels of habitat loss compared with high levels ($\frac{1}{6}$ vs. $\frac{2}{3}$, respectively), we predicted a significant difference in total abundance between the 3 arrangements for a window of intermediate dispersal rates (Figure 3). For either very small or very large locomotion rates, the theoretical growth rate will be near its maximum or baseline, respectively, so we expected little difference in the total abundance across arrangements with the same total available food.

Experimental

With low levels of habitat loss (5 of 6 coverage), the main effect of locomotion was significant ($p < 0.0001$, $F = 13.618$). There was a greater abundance of the slow-moving strain than the others. The main effect of fragmentation was also significant ($p = 0.0257$, $F = 4.098$). The slow-moving strain had significantly greater abundance under low levels of fragmentation than the slow-moving strain under high fragmentation ($p = 0.0270$, $t = 3.1342$) (red box in Figure 4a). With high levels of habitat loss (2/6 coverage), the main effect of locomotion remained significant ($p < 0.0001$, $F = 17.8443$); there was a greater abundance of the slow-moving strain than other trains. Consistent with the low levels of habitat loss case, only the slow-moving strain showed significantly greater abundance under low levels of fragmentation compared with the high levels of loss ($p = 0.0243$, $t = 2.8305$), and abundances under medium fragmentation were more than under high levels of fragmentation, although the difference was not significant (red box in Figure 4b). The effect of habitat loss on abundance was weakly significant ($p = 0.0619$) under low levels of fragmentation, moderately significant ($p = 0.0246$) under medium levels of fragmentation, and strongly significant ($p < 0.0001$) under high levels of fragmentation. The effect of locomotion was significant ($p = 0.0002$) under low levels of fragmentation, moderately significant ($p = 0.0203$) under medium levels of fragmentation, and strongly significant ($p < 0.0001$) under high levels of fragmentation (Appendix S2).

The correlation slopes between distance to food and abundance varied significantly among the 3 locomotion levels ($p < 0.0001$), and the significant variation was consistent across different levels of fragmentation and habitat loss. We detected negative correlations between population abundance and distance to food for slow and intermediate movers (red and green

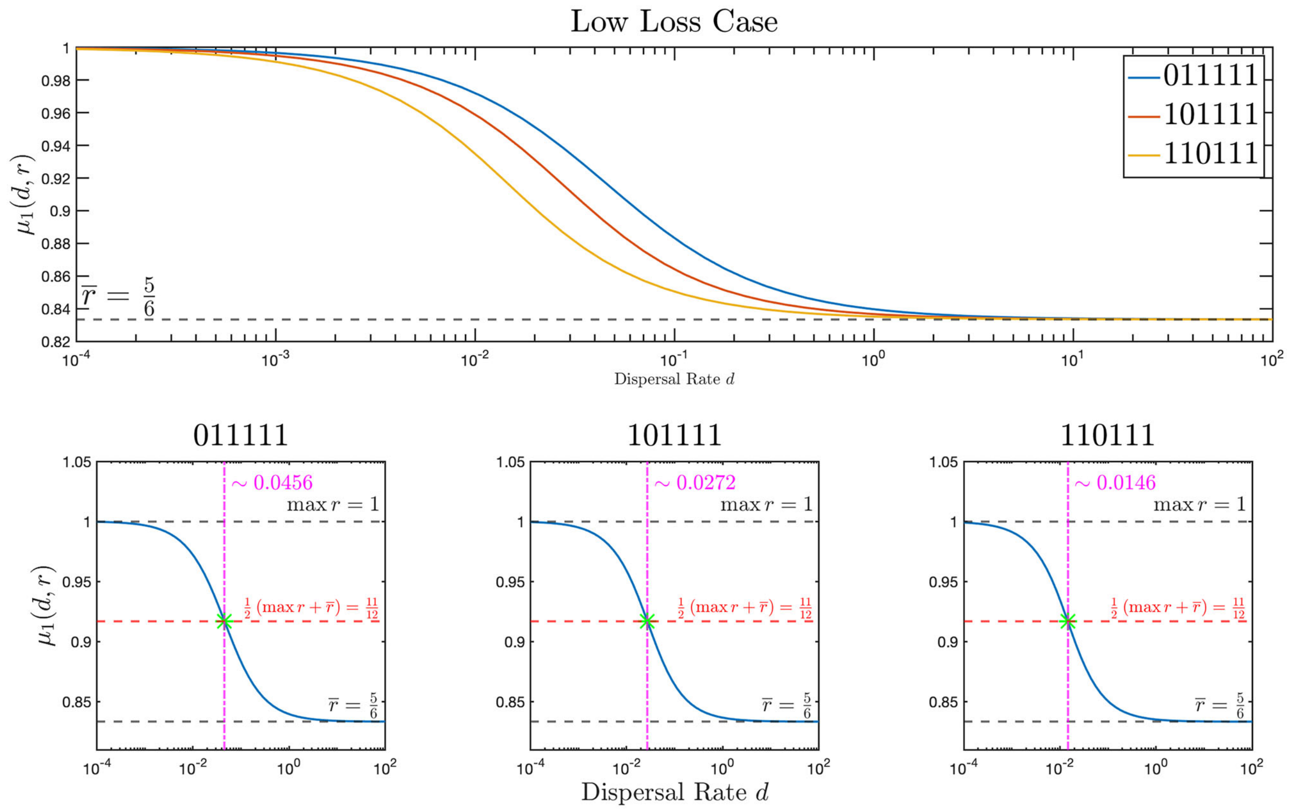

FIGURE 3 Theoretical growth rate of the nematode population ($r_{\text{eff}}[d, r]$) predicted by Equation (4) versus the dispersal rate (d) for 3 cases of low levels of habitat loss and the relationship between different arrangements of nutrient (1, with food; 0, without food) and fragmentation length scale (d_{frag}) (vertical dashed pink lines) predicted by Equation (4) for each experimental arrangement displayed in the top panel.

in Figure 5), with a stronger negative correlation where levels of habitat loss were high. Correlations were weaker between population abundance and distance to food for fast movers than for slow and intermediate movers. Together, our results supported our mathematical findings that fast dispersal rates create greater mismatch between the population and the resource distribution, whereas slower dispersal rates enable most of the population to remain in close to the food source (blue lines in Figure 5).

DISCUSSION

Our findings demonstrate how species characteristics, such as locomotion rate, can affect how they are affected by fragmentation changes. The difficulty of testing different levels of habitat fragmentation in natural systems and precisely measuring the subsequent impacts has led to vastly different interpretations of fragmentation's effects on biodiversity and species abundance (Fletcher Jr. et al., 2018). And, such tests are costly and can take years to complete, a luxury we do not have in the face of accelerating habitat loss (Díaz et al., 2020). As such, there is substantial value in assessing the outcomes of populations in an experimental setting, as we did. By studying the total abundance outcomes in a more easily controllable experimental setting, one can measure the impact of habitat fragmentation in relation to the total available habitat on species with different motility rates.

Taking advantage of our experimental system, we distinguished the effect of habitat loss and habitat fragmentation on population dynamics under low (~80% resource coverage) and high (~30% resource coverage) levels of habitat loss. Our theoretical results showed that spatial configuration and the total amount of habitat are critical factors in determining species' effective growth rates; population abundance decreased consistently when fragmentation increased and the total amount of habitat loss was held constant. However, such findings come with important caveats. Although differences were observed for high and low levels of habitat loss, the relative differences between the best- and worst-case scenarios (in terms of the effective population growth rate) were more robust for high levels of loss than for low levels. This can be seen in Figures 3 and 4, where $\overline{r}$ is (relatively) much smaller under high levels of habitat loss cases than under low levels. From the theoretical perspective, this is unsurprising because there was simply more habitat available and fewer ways to fragment the environment to negative effect.

Similarly, the effect of habitat fragmentation was also stronger when habitat loss increased, consistent with findings of Rybicki et al. (2020). This can be seen in Figures 2 and 3 when

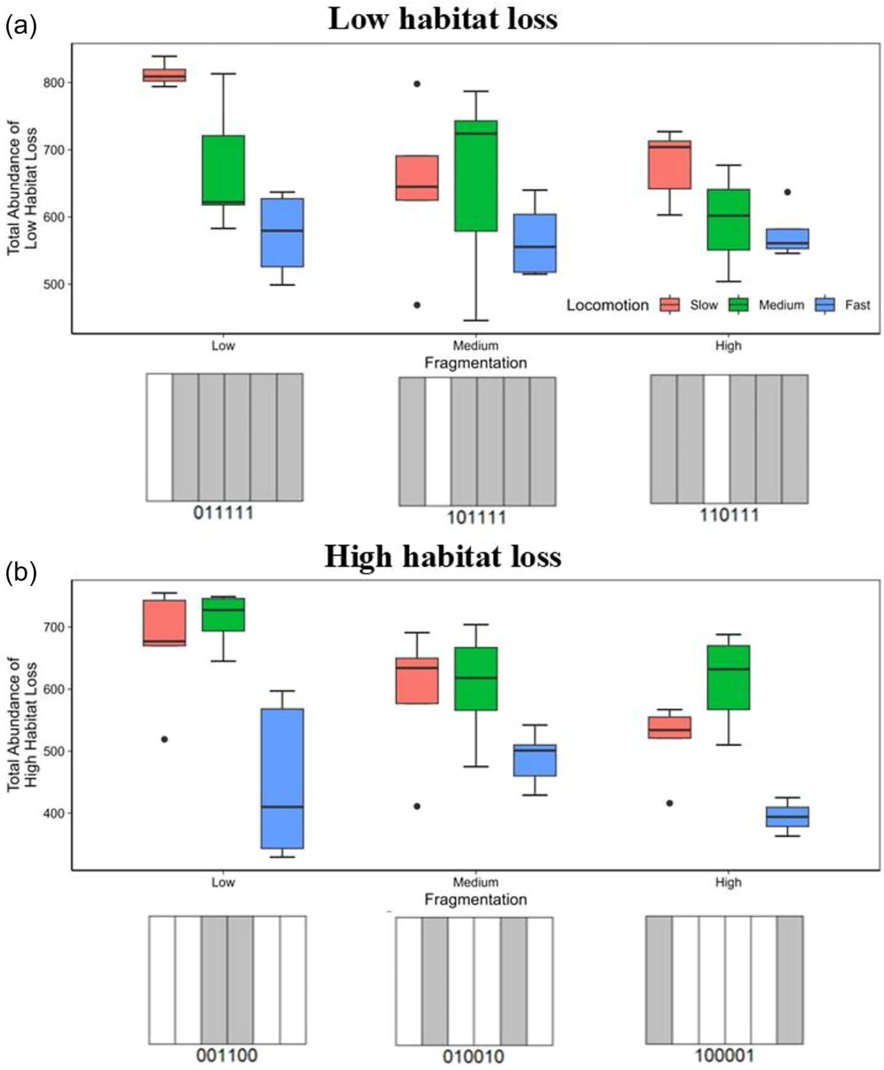

FIGURE 4 (a) Total population of strains of *Caenorhabditis elegans* with 3 different locomotion rates in a scenario with little habitat loss (5 of 6 habitats intact) and 3 levels of fragmentation (low, 011111; medium, 101111; high, 110111) and (b) total population of strains with different locomotion rates in a scenario with much habitat loss (2 of 6 habitats intact) and 3 levels of fragmentation (low, 001100; medium, 010010; high, 100001) (error bars, standard error). Grayscale graphs show the 6 designed fragmentation environments (gray columns, areas with food; white columns, areas without food).

one compares the differences among the blue, red, and yellow curves. However, the gap between these curves was greater for high (Figure 3) than low levels of habitat loss (Figure 3). This is consistent with our empirical findings, which suggest that fragmentation can have a negative effect on population growth and abundance not only when the amount of remaining habitat is low but also when habitat coverage is high. However, only the abundance of slow-moving strain was significantly greater under low levels of fragmentation than under high fragmentation in both habitat coverages. Hence, both our theoretical and empirical results can improve understanding of the habitat amount hypothesis, which suggests that a single predictor variable, namely habitat amount, should be used when analyzing species richness (Fahrig, 2013).

Consistent with Rybicki et al.'s (2020) conclusions, our findings suggest that the effects of fragmentation were more significant for lower levels of habitat amount (20–30%) than higher levels (60–80%). They also suggest that habitat amount alone is not a reliable predictor variable when the existing amount of habitat is already low. The degree to which habitat amount can act as a lone predictor variable depended on the locomotion strategies and abilities of species considered. For example, very slow and very fast movers had comparable effective growth rates, and the differences were sometimes significant for intermediate locomotion speeds (Figures 2 & 3). Our results contradict the previous understanding that when the total habitat amount is fixed, increasing fragmentation results in a positive effect due to a reduction in patch isolation. In our model, the reduction in size of connected habitat patches had a negative effect that was not compensated for by a gain in connectivity between patches. Our theoretical developments, particularly the fragmentation assessment

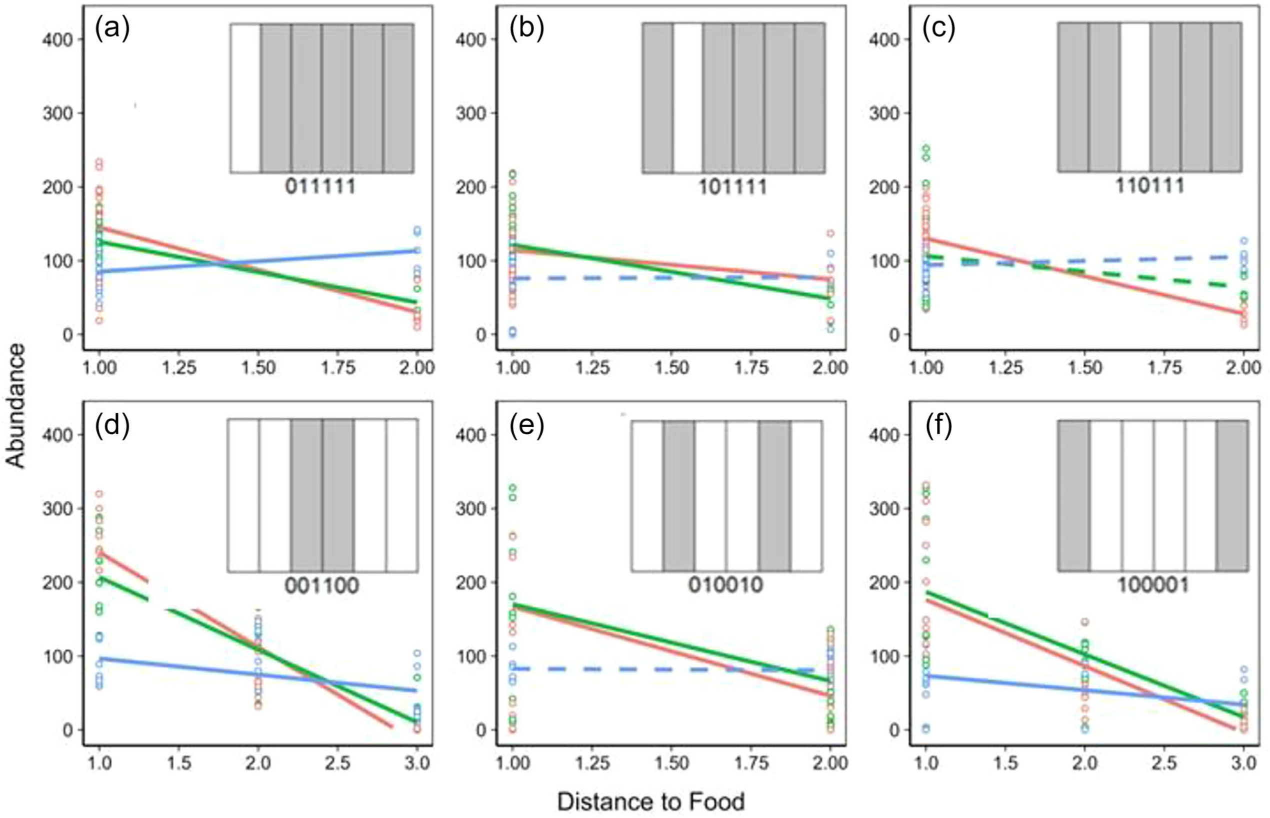

FIGURE 5 Correlation between *Caenorhabditis elegans* abundance and distance from food in the (a–c) little habitat loss (011111, 101111, and 110111, respectively; 1, food present; 0, food absent) and (d–f) much habitat loss (001100, 010010, and 100001, respectively) (red, slow mover; green, intermediate mover; blue, fast mover; solid lines, significant correlation between abundance and distance to food at a significance level of 0.05; dashed lines, nonsignificant correlations between abundance and distance to food at a significance level of 0.05). Grayscale graphs show the fragmentation environment (gray columns, food present; white columns, food absent).

quantity d_{frag}, further support this idea. Therefore, our results suggest that the degree to which fragmentation affects a dispersing population hinges on the scale of unconditional dispersal relative to the scale of the patchiness of the habitats (Adler & Nuernberger, 1994; Frank & Wissel, 1998). Together, our separation of habitat fragmentation from habitat amount is supported by a recent review literature that suggests more work on fragmentation will dissipate confusion in habitat fragmentation research (Riva et al., 2024). Most notably, perhaps, is our contribution to an understanding of when and why habitat fragmentation is, in our case, more negative or more neutral.

Our empirical and modeling data demonstrated a new phenomenon that has yet to be identified in a natural system: dispersal rates play an important role in how well the species adjust to fragmented habitat conditions. Our results highlighted that the population abundance of slow movers continuously decreased when fragmentation increased in both the low and high habitat loss cases. Martin et al. (2023) concluded from extracting data from 90 papers, there was insufficient support for using weak dispersal as a general indicator of species risk in human-modified landscapes. Our work, therefore, provides solid theoretical and empirical support that weak dispersers are more prone to risk from fragmentation than strong dispersers. In addition to supporting the previous understanding that the effects of isolation may appear mainly in landscapes with a very fragmented habitat for mobile organisms (Andren, 1994), our empirical data and modeling formulations showed that a higher rate of dispersal maintained a stable but lower population abundance than a slower rate of dispersal. One possible explanation for this is that fast movers spend nearly an equal amount of time across the entire Petri dish, whereas the slow and intermediate movers concentrate more on areas with food than on areas short of food (Figure 5). This is readily observed in Figures 2 and 3, where the fast diffuser is close to the baseline theoretical growth rate for large motility rates, regardless of the arrangement of habitat. Alternatively, a higher dispersal rate may require more energy to be spent on movement, even when food is abundant. Although this may allow them to seek resources more easily, there can be a subsequent trade-off between dispersal rate and energy use (Weigang & Kisdi, 2015). Consequently, our results support the hypothesis that aggregated loss in patchy habitats can harm populations, at least at scales of relevance to dispersal, by creating greater isolation at the mesoscale across landscapes (Chesson, 2000; Fletcher Jr. et al., 2023; Melbourne et al., 2005). This reveals an intimate relationship between the degree of fragmentation in the landscape and the rate of locomotion of the species (Tao et al., 2024).

There is an unprecedented opportunity for empirical and theoretical movement ecology to contribute to conservation potential in an era of rapid, human-induced global change. Our results have important conservation implications. For one, the degree of fragmentation of a landscape and the need for human intervention need to be considered relative to the movement rate of the residential species. Our results suggest that in landscapes with a highly fragmented habitat, a further reduction in habitat amount can have compounding negative effects if total habitat is already low, at least for low motility rates. Thus, in landscapes with highly fragmented habitats, the spatial arrangement of patches can be important. In contrast, one may not observe significant differences in practice if the motility rate is already large in relation to the scale of fragmentation in the landscape. In natural habitats, even minor changes (such as a 40-m unpaved road in the middle of a forest) can alter community structures dramatically, and intact forests contain more species per unit area than small, more isolated fragments (Laurance et al., 2002, 2011).

One possible explanation for these seemingly opposing insights are species-specific traits. We found differences between differing dispersal strategies and a connection between the dispersal rate and the scale of habitat fragmentation. Therefore, we cannot consider habitat fragmentation in a vacuum: species-specific traits, intrinsic to the concept of habitat itself (Hall et al., 1997), are intimately connected to the resulting impacts of habitat fragmentation on population growth rates and abundance. Ultimately, understanding how organisms with different traits respond to fragmentation could improve conservation of biodiversity. This highlights a limitation in generalizing these insights to the natural world based on our modeling framework. Although purely diffusive movement for a single, isolated nematode population over a relatively short timescale for a fixed habitat arrangement is a reasonable first step to explore the connections between our theoretical and empirical results, our assumptions are not expected to be sufficient given the complexities of the natural world. Despite this limitation, our theoretical framework provides preliminary validation to the approach and is broadly generalizable beyond the minimalistic assumptions made here. For example, in the natural world, one expects at least 3 influential factors we did not consider: different movement strategies, species–species interactions, and a gradual change in the environment over time. A wide range of movement strategies falls within the more general framework of uniformly elliptic operators. For example, one may incorporate environment-specific dispersal rates (e.g., slower in favorable habitat, faster in less favorable matrix) or directed movement toward or away from stimuli. In cases where there are multiple populations interacting in a cooperative rate, such as a population switching between multiple physiological states, an effective population growth rate can still be obtained in principle, although the technicality involved in the extension may be more suitable for a numerical exploration. This allows for the inclusion of additional community-level interactions.

One may also consider the consequences over larger timescales by investigating the total abundance at steady state under different movement strategies or fragmentation regimes. In such a case, density dependence is included, and a positive population growth rate will ensure a trend toward some steady-state profile when the resources are assumed temporally constant. Theoretical models also exist that consider time-varying environments so that one may incorporate resource depletion effects, further complicating the formal analyses but perhaps providing added realism (Cantrell & Cosner, 2004). Such theoretical perspectives are intriguing. We hope our work will provide motivation and enthusiasm to extend such empirical study to different organisms and different environments amenable to the theoretical framework we introduced, with the ultimate goal of understanding and predicting the impacts of habitat loss and fragmentation based on basic organismal traits alone.

AUTHOR CONTRIBUTIONS

Jamaal Jacobs, Yurij Salmaniw, Hao Wang, and Bo Zhang designed the study and experiments. Jamaal Jacobs collected experimental data. Yurij Salmaniw and King-Yeung Lam performed mathematical analysis. Lu Zhai performed statistical analysis. Jamaal Jacobs, Yurij Salmaniw, King-Yeung Lam, and Bo Zhang wrote the first draft, and all authors revised the manuscript.

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SUPPORTING INFORMATION

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